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SKULLS AND BRAINS OF SOME MAMMALS FROM THE *NOTOSTYLOPS* BEDS OF PATAGONIA[1]

BY GEORGE GAYLORD SIMPSON

Mammals of the *Notostylops* Beds, the earliest mammals yet described from South America, are very poorly known, and the literature, aside from the publications of Ameghino, generally either neglects them or is very uncomprehending concerning them. This is due to several causes: the fragmentary nature of most of the known specimens, neglect or distrust of Ameghino's work, and the fact that this work was in large part of a preliminary nature and inadequately illustrated. This last point could not well be appreciated without revision of the Ameghino Collection, which proves to contain a number of fine specimens which have been illustrated only in part or not at all. In advance of fuller revision, it therefore may be of interest to publish a few sketches of the skulls of the best known species in that collection. These will later be augmented by drawings of skulls of several other species found by the Scarritt Patagonian Expedition. Of the four genera here illustrated, there are previous figures of the skull of only one, *Notostylops*. It is also now possible to give figures of partial endocranial casts of *Notostylops* and of *Oldfieldthomasia*.

I am much indebted to the authorities of the Museo Nacional de Historia Natural of Buenos Aires, and particularly to the director, Dr. M. Doello-Jurado, and also to Sr. Carlos Ameghino for the privilege of studying this material. The restoration (but not the skull) of *Notopithecus* was drawn by Louise Germann, the endocranial cast of *Oldfieldthomasia* by Mildred Clemans, and the other illustrations by me. In these drawings an attempt has been made to correct distortion, and they are in part composite, as noted in the text, but the parts in continuous lines are carefully delineated from actual specimens and are not diagrammatic or conjectural.

THE SKULL OF **Arminiheringia**

Arminiheringia auceta is the most completely known pre-Santa Cruz "sparassodont" or borhyænid, but it has not been figured, and Ameghino's brief description did not lead to recognition of its peculiar

[1]Publications of the Scarritt Patagonian Expedition, No. 10.

character. It therefore seems worth while to illustrate the species in this preliminary note, even though the cranial part of the skull is not known. The originals are the types, Museo Nacional Nos. 10972 and 10970, face and lower jaws respectively, found separated in the Ameghino Collection but both included in the original description and, on this and also independent evidence, almost surely of one individual. In the figure some distortion has been corrected but nothing has been added.

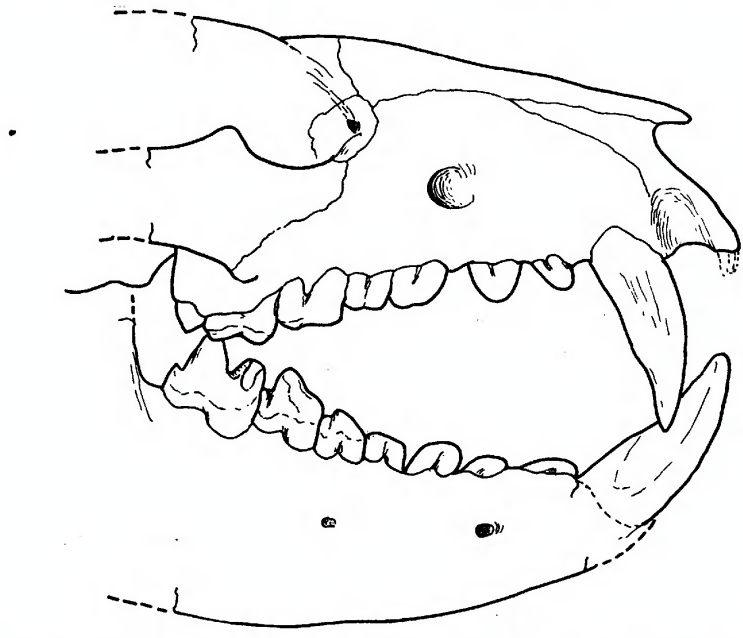

Fig. 1.—*Arminiheringia auceta* Ameghino. Museo Nacional No. 10972 (skull) and No. 10970 (jaws). Front part of skull and jaws, right lateral view. One-half natural size.

The presence of this great specialized carnivorous marsupial in the *Notostylops* Beds is very remarkable and unexpected. With the exception of a much later and amazingly aberrant genus found by Riggs in Catamarca, *Arminiheringia* appears to be the most specialized known borhyænid. It is a large animal, a third larger than *Borhyæna tuberata* and about the size of the great *Pharsophorus lacerans*.

The face is much like that of other large borhyænids, e.g., *Borhyæna* itself, but is somewhat more elongate, a feature reflected in the long posterior projection of the premaxilla. The naso-lacrymal contact, typical of the family, is already established. The mandible is extra-

ordinary for its long, almost cylindrical and horizontal symphysis, extending back to the posterior end of M_1. Aside from being of the most specialized type, as seen also in *Borhyæna*, with strongly reduced protocone, no metaconid, and talonid reduced to a small cingulum-like heel, the molars are not very distinctive. In keeping with the long rostrum, the premolars are well spaced. Most remarkable are the canines. The upper canines are large and slightly procumbent rather than recurved. The lower canines still larger and strongly procumbent, shearing between the upper canines and at nearly a right angle to them at the beginning of the bite. The root extends very far back, at least to M_1, and those of the

Fig. 2.—*Notostylops brachycephalus* Ameghino. Museo Nacional No. 10499 (skull only). Lower jaw composite. Skull and jaws, right lateral view. Two-thirds natural size.

two canines are closely appressed anteriorly, almost in contact. The crowns diverge somewhat, but crowd the two pairs of small lower incisors so that the first pair is anterior to and not between the second.

The presence of so large and specialized a borhyænid in so ancient a fauna bespeaks a great antiquity for the group. This, however, might be overemphasized. Although distinctly more specialized than even the known Santa Cruz forms, it is not greatly so and is orthodox, that is, presents no wholly unique or profoundly different characters of kind but only modifications of degree. It is also to be noted that these beds do contain borhyænids distinctly more primitive than any known later

forms. *Arminiheringia* is an early, markedly but somewhat superficially specialized offshoot. Analogous cases are abundant in the ancient North American faunas, e.g., *Triisodon* among carnivores or *Periptychus* among ungulates.

The Skull of **Notostylops**

The skull of *Notostylops* has been figured by Ameghino,[1] a dorsal view of a poor skull and palatal view of an excellent one, as well as views of a good lower jaw. Patterson[2] has given ventral and lateral views of the otic region.

The present figure shows the lateral view of Ameghino's fine skull, type of *Notostylops brachycephalus*, Museo Nacional No. 10499, which is unique in being not only nearly complete, but also nearly uncrushed. The mandible shown is a composite of several jaws of this or very closely related species.

Perhaps because of its fame as godfather of this early fauna, *Notostylops* is frequently considered an unspecialized notoungulate and stressed in general discussions of notoungulate origin. It is primitive in many respects, but it is not generalized. On the contrary, it is one of the most especially adaptive forms of the fauna. The habitus is somewhat more rodent-like than ungulate-like, and it probably occupied more or less the ecological status of the larger rodents (rodents being absent in the fauna), as the cænolestids and polydolopids did of the smaller.

As opposed to a generalized notoungulate structure, the skull of *Notostylops* is especially characterized by its short, high rostrum and long, wide, powerful cranium and zygomata. In spite of the development of diastemata, the rostrum is short and the orbit is anterior to the middle of the skull, rather than median or slightly posterior. The anterior root of the zygoma is opposite P^4 and M^1, rather than M^{2-3} which is the primitive position. The zygomata are well expanded and powerful, and sagittal and lambdoid crests well developed.

The lower jaw is not distinctly rodent-like, the parallel axes of horizontal ramus and tooth-row, elevated condyle, and broad flat angle being more ungulate-like.

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[1]Ameghino, F. 1897. Mammifères crétacés de l'Argentine. Deuxième contribution à la connaissance de la faune mammalogique des couches à *Pyrotherium*. Bol. Inst. Geog. Argentino, XVIII, pp. 406–429, 431–521. [Fig. 68, dorsal view, partial skull of *Notostylops murinus*. Figs. 69–70, crown and lateral views of good lower jaws placed in same species.]

1906. Les formations sédimentaires du Crétacé Supérieur et du Tertiaire de la Patagonie. An. Mus. Nac. Buenos Aires, XV [(3) VIII], pp. 1–568. [Fig. 179, palatal view of skull of *Notostylops brachycephalus*.]

[2]Patterson, B. 1932. The auditory region of the Toxodontia. Field Mus. Nat. Hist., Pub. 305, Geol. Ser., VI, No. 1, pp. 1–27. [Fig. 2, referred to *Notostylops aspectans*.]

One pair of incisors, $I\frac{1}{2}$, is enlarged in each jaw, but still not fully rodent-like. They form roots, and the lower incisor works against the upper so that they are nearly at right angles, and the former is truncated almost transversely, not developing a chisel-edge. The other incisors, canine, and first premolars are always reduced in size and of simple

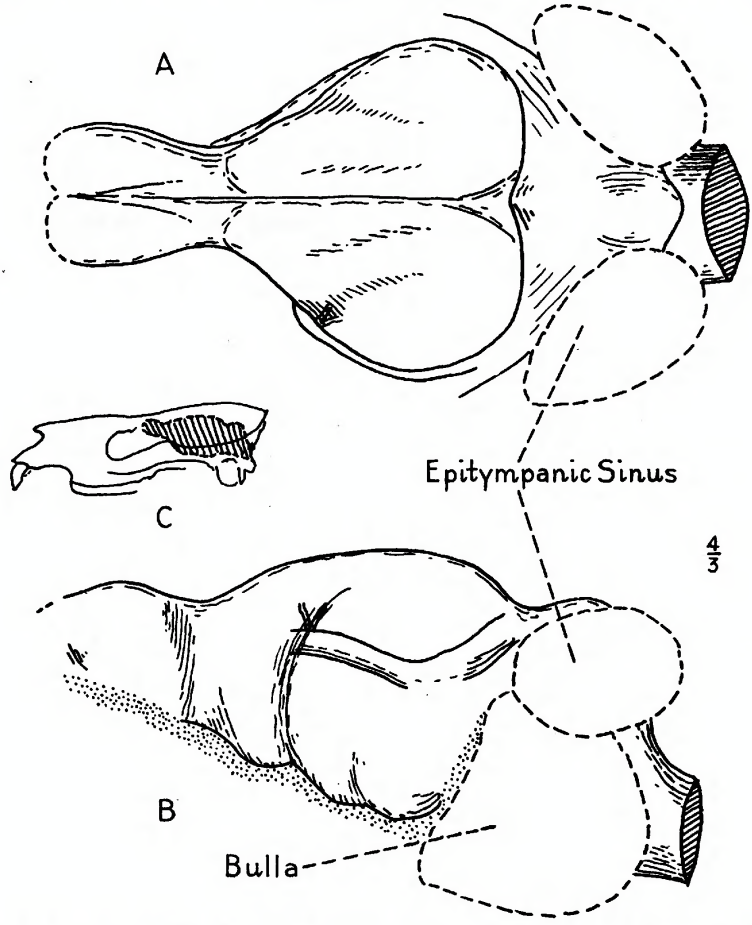

Fig. 3.—*Notostylops escaridus* Ameghino. Museo Nacional No. 10506. A, Endocranial cast, dorsal view. B, Same, left lateral view. C, Diagram of skull and brain cavity. A and B, four-thirds natural size. C, two-ninths natural size.

form, but the numerical reduction is highly variable, a variation which I believe to be largely individual although probably as a tendency it is in part taxonomic. In the individual illustrated, for instance, the upper canine was present on one side and not on the other. The cheek teeth

have crowns of moderate height, but they are remarkable in having shallow coronal patterns, so that the upper molars rapidly become worn in such a way that they present only a concave dentine surface surrounded by a simple enamel border. This rapid disappearance of the coronal folds and lophs would appear to be disadvantageous, especially in an animal which seems to have fed on very abrasive vegetable substances. Perhaps this had an influence on the early extinction of the family and its ecological replacement by others which rapidly became efficiently hypsodont.

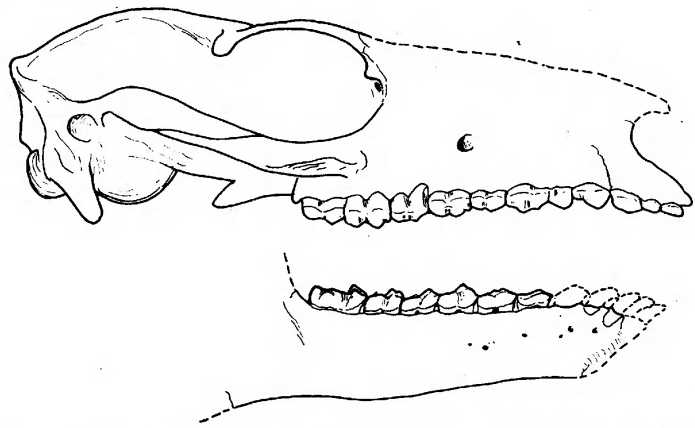

Fig. 4.—*Oldfieldthomasia debilitata* (Ameghino). Museo Nacional No. 10376 (skull only). Jaw composite. Skull and jaws, right lateral view. Three-fourths natural size.

The Endocranial Cast of **Notostylops**

Mus. Nac. No. 10506 includes a natural internal cast of a skull referred to *Notostylops escaridus* which with some preparation has revealed the essential endocranial characters. So far as I know, the only other published notoungulate brain casts are those of *Typotherium* and of *Toxodon*, both Pleistocene, figured by Gervais (1872),[1] copied and discussed by Edinger (1929).[2] The cast of *Notostylops* bears very little resemblance to the large, specialized *Toxodon* but is very similar to *Typotherium*.

The cast of *Notostylops* is of strikingly primitive character, with some resemblance to condylarths on the one hand and rodents on the other.

[1]Gervais, P. 1872. Mémoire sur les formes cérébrales propres à différents groupes de mammifères. Journ. Zool., I, pp. 425–469.

[2]Edinger, T. 1929. Die fossile Gehirne. Ergeb. Anat. u. Entwick, XXVIII, pp. 1–249. [Standard work on the subject, with very full annotated bibliography and copies of most figures, including those of Gervais, above.]

This is harmonious with its dental and osteological characters, which are those of a rather primitive ungulate convergent toward a rodent habitus. The olfactory bulbs are very large, fully exposed, and extend straight out anterior to the cerebrum. The latter is simple, pyriform, much constricted anteriorly and with greatest width posterior to the middle. In dorsal view there are only two distinct sulci. One starts on the dorsal surface, near the middle of its greatest expansion, and passes forward and outward, becoming more distinct, then down around the sides of the anterior part of the cerebrum. This appears to be the fissura sylvii. Between this and the midline, confined to the dorsal surface, is a shorter and less distinct, nearly straight longitudinal sulcus, similar to the sagittal sulcus of *Typotherium* and of many rodents.

The dorsal features of the cerebellum are not clear, and it does not appear to have been very closely applied to the bone. It was broadly exposed and had a little over half the dorsal length of the cerebrum, below which it seems to have been moderately depressed. From this vague cerebellar region, a large vascular sinus runs around the cerebrum on each side, to about the fissura sylvii where it gives off two much smaller vessels directed upward.

Large roughly egg-shaped epitympanic sinuses overlie the cerebellar region dorsolaterally, and still larger and more irregular bullæ laterally and ventrolaterally.

The whole brain occupies about one half the length of the skull, related to the advanced orbits and relatively long cranial part, as noted above.

The Skull of **Oldfieldthomasia**

Ameghino figured teeth of this genus, but the skull has not previously been figured. The accompanying drawing is based on the type of *O. debilitata* (by Ameghino placed in the genus *Acœlodus*[1]), No. 10376 in the Ameghino Collection in the Museo Nacional. It is well preserved except for dorsoventral crushing and loss of the nasals. The lower jaw is composite, based on several lower jaws surely of this genus and either of this or closely related species.

Oldfieldthomasia comes closer than either *Notostylops* or *Notopithecus* to being a really generalized notoungulate.

The most striking peculiarities are the relatively long rostrum and the large orbit placed posterior to the middle. The zygoma arises

[1]It is not proposed to enter into taxonomy here, but it may be noted that *Acœlodus* is a very poorly defined genus and that even if it is really separate from *Oldfieldthomasia* the species *debilitata* belongs in the latter. The type of the genotype of *Oldfieldthomasia* has *five* upper premolars but this is surely an anomaly, or possibly even an artifact, and not a valid character.

opposite M^{2-3} and is slender and relatively feeble. The mandible is unusually long and slender.

The teeth are fully brachyodont, in complete number, and form a closed and rather evenly graded series. The canines are incisiform. In spite of the very different aspect of their more extreme forms as illustrated here, the families Acœlodidæ and Notopithecidæ are apparently closely related, and there are genera which might be placed in either. As they appear to be related to lines wholly distinct in later faunas, this tendency to merge in the *Notostylops* Beds is one of numerous lines of evidence suggesting that the divergence of the Notoungulata was not long anterior.

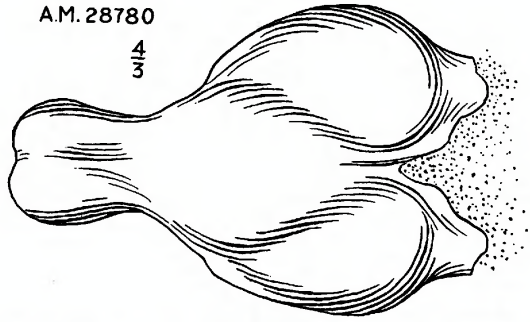

Fig. 5.—*Oldfieldthomasia* sp. Amer. Mus. No. 28780. Endocranial cast, dorsal view. Four-thirds natural size.

The Endocranial Cast of Oldfieldthomasia

Of this genus we have an endocranial cast, Amer. Mus. No. 28780, referred to *Oldfieldthomasia* sp., by no means so well preserved as that of *Notostylops* just described, but showing most of the essential dorsal characters.

In general character, this brain is very like that of *Notostylops*, the only striking difference being the relatively smaller olfactory lobes; in *Notostylops* they are well over half the length of the cerebrum, and in this form somewhat less than half. Their position and full exposure are the same. The fissura sylvii is similarly developed, and seems to communicate with a more posterior dorsal fissure, and thus more fully to outline a posterolateral lobe, but this is not wholly certain. The sagittal dorsal sulcus is not clear, and may be absent. Part of a lateral vascular sinus, similar to that of *Notostylops* but relatively smaller, is visible near the fissura sylvii, and there is also preserved part of a median dorsal sagittal sinus.

The fundamental resemblance of the endocrania of *Notostylops*, *Oldfieldthomasia*, and the much later *Typotherium* strongly suggests that they represent a primitive, characteristic notoungulate type of brain, from which the more highly modified (but still relatively archaic) brain of *Toxodon* was probably derived. The modification of the latter appears

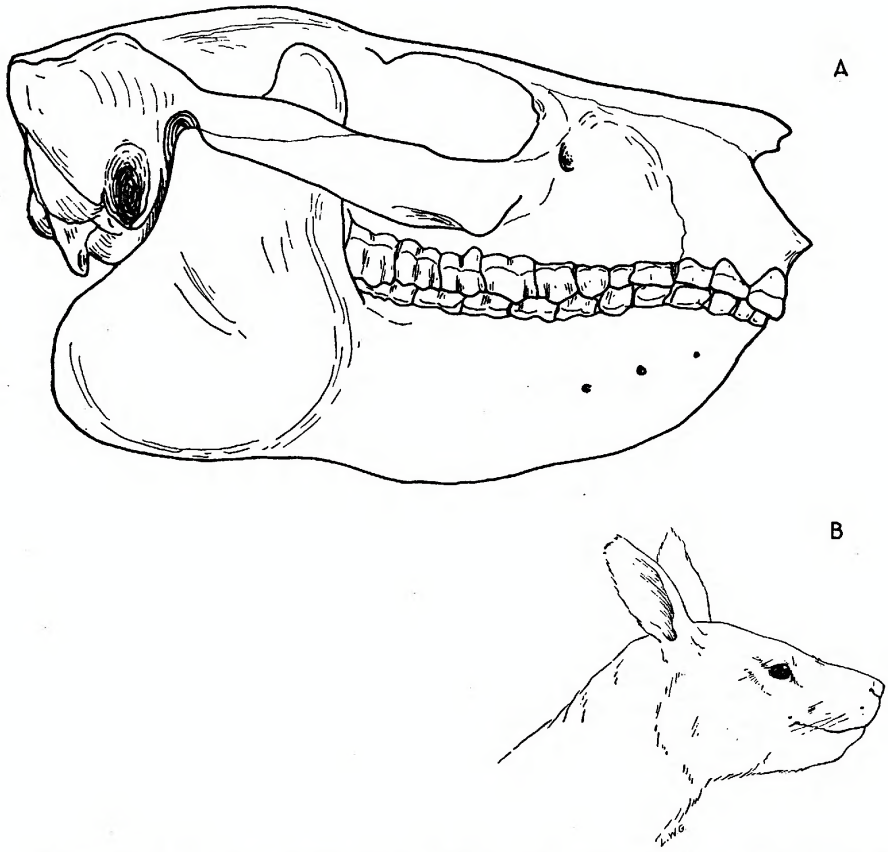

Fig. 6.—*Notopithecus adapinus* Ameghino. Museo Nacional No. 10787. Skull and jaws, right lateral view, one and one-half times natural size, and restoration one-half natural size.

due to change of habits—it is much less macrosmatic—and to mere bulk rather than to markedly superior quality, and so far as this scanty but very suggestive evidence goes, it is fair to conclude that the notoungulates were mentally unprogressive. Certainly they appear to be much less progressive than the artiodactyls or perissodactyls, and this

fact is very interesting in view of their extinction when brought into direct competition with those two groups.

The Skull of **Notopithecus**

A number of good skulls of this genus are known, but none has previously been figured. The present illustration is based on Museo Nacional No. 10787, nearly complete associated skull and jaws referred to *N. adapinus*, with minor additions from other specimens of the same common species.

The skull is short, broad, and deep. In spite of an equal shifting forward of the zygomatic root, to opposite P^4–M^1, the orbit is less definitely anterior to the middle than in *Notostylops*, as the cranium is relatively less elongate and the nasals less retracted. The orbit and brain case are relatively larger, probably simple functions of smaller absolute size. In spite of a different adaptive tendency, there is a distinct heritage resemblance to *Notostylops* and to *Oldfieldthomasia*, which suggests that the time of divergence was not long anterior. In one respect, the inflation of bulla and temporal region, the skull is very highly and, in a manner of speaking, prematurely specialized. Such inflation is a nearly constant notoungulate character, but it here reaches its maximum relative to the total size, probably in part again a function of the small absolute size, but perhaps in part aberrant.

The mandible is noteworthy for its great depth (although relatively very thin transversely) and the enormous expansion of the angular region.

Although apparently advancing in a different direction and with a very different ultimate destiny, the dentition is still very like that of *Oldfieldthomasia*, that is, little removed from the ancestral notoungulate type. The crowns are higher than in *Oldfieldthomasia*, and the coronal pattern more deeply impressed than in *Notostylops*, but the dentition is still brachyodont. As in *Oldfieldthomasia*, it still forms a complete closed and almost evenly graded series, with incisiform canines. The first upper incisors, rather than the third, are slightly enlarged, a prophetic character, while the three lower incisors are of nearly equal size. The occlusion is noteworthy: $I_{1\text{-}2}$ occlude chiefly with I^1, I_3 wholly with I^2, and the lower canine wholly with I^3, less aberrant relations being reached only with P_3 which occludes between P^2 and P^3 as is usual.

This very interesting genus unquestionably lies in or near the ancestry of the Typotheria. Its skull characters lack little of being as specialized as those of the least advanced Santa Cruz forms, although

even the latter present few really important modifications of the generalized notoungulate skull. The dentition of *Notopithecus*, on the contrary, is very much more primitive than in any known later typotheres and suggests either very rapid progress or an unexpectedly long lapse of time between the *Notostylops* and *Pyrotherium* Beds. There are no fully hypsodont mammals in the *Notostylops* Beds, and most, like *Notopithecus*, are definitely brachyodont, even when, as in this case, their direct or collateral descendants early acquired complete hypsodonty.